

Updated phylogeny, taxonomy, and diversification of *Janthecla* Robbins & Venables (Lycaenidae: Theclinae: Eumaeini)

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Abstract. The phylogeny of *Janthecla* is updated using new information on outgroups and adding two newly described species from the Upper Amazon Basin. Evidence that *Allosmaitia* and *Laothus* are the closest relatives of *Janthecla* is outlined. *Janthecla adrienne* Robbins **n. sp.** is described from wet lowland rain forest in Peru, and *Janthecla halli* Busby & Robbins **n. sp.** is named from rain forest in Ecuador. Topology of the updated cladogram is essentially the same as in the original analysis, but a new synapomorphy for *Janthecla* is identified. *Janthecla adrienne* is sister to the remainder of *Janthecla* except for *J. rocena*. *Janthecla halli* belongs to the nine-species *J. sista* clade, which is not well resolved phylogenetically. *Janthecla adrienne* has upturned frons scales, a trait that is otherwise shared in the Eumaeini only with some species of *Laothus* and *Evenus*. The relatively rapid diversification within the *J. sista* clade is discussed.

Key words: butterflies, frons, hairstreaks, Lepidoptera, Neotropics.

INTRODUCTION

Janthecla Robbins & Venables (Lycaenidae: Theclinae) is a ten-species Neotropical eumaeine genus that primarily inhabits wet lowland forest (Robbins & Venables, 1991). Although most species have a similar ventral wing pattern, the only identified synapomorphy was a structural detail of the female genitalia (Robbins & Venables, 1991). *Janthecla rocena* (Hewitson) ranges from Mexico to southern Brazil, but eight lowland and one cloud forest species have more restricted distributions. The outgroup for a 1991 phylogenetic analysis based on adult morphological characters was "all other eumaeines" because close relatives of *Janthecla* were unknown (Robbins & Venables, 1991). The analysis resulted in few well resolved nodes (Robbins & Venables, 1991).

New information provides the opportunity to update and expand this analysis. *Janthecla* was recently placed in the *Allosmaitia* Section of the Eumaeini along with *Allosmaitia* Clench and *Laothus* K. Johnson, Kruse & Kroenlein (Robbins, 2004b). Also, two new species of *Janthecla* have been discovered in the Peruvian and Ecuadorian Amazon (Robbins, 2004b).

It is the purpose of this paper to infer phylogenetic

relationships among *Janthecla* species (including the newly described ones) using *Allosmaitia* and *Laothus* as outgroups, to describe the two new species, to discuss new character evidence from these species relating to the *Allosmaitia* Section, and to use this updated information to examine diversification within *Janthecla*.

MATERIALS AND METHODS

In addition to collections seen previously (Robbins & Venables, 1991), new data were recorded from *Janthecla* specimens in Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM), Universidade Federal do Paraná, Curitiba, Paraná, Brazil (DZUP), Museo Ecuatoriano de Ciencias Naturales (MECN), Quito, Ecuador, National Museum of Natural History, Washington, DC, USA (USNM), Oregon State University (OSU) and the private collections of Robert C. Busby (RCB), and Jason Hall and Keith Willmott (JHKW).

Standard entomological techniques were used (Robbins & Venables, 1991). Genitalic terms follow those in Klots (1970), as illustrated in Robbins (1991), and wing vein terminology follows Robbins and Venables (1991). Forewing lengths were measured with a vernier caliper and reported statistically as a mean and standard deviation (SD) with sample size (N). The data

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Table 1. Character matrix (14 taxa, 13 characters) for *Janthecla* including outgroups *A. coelebs* and *L. barajo*. The characters were modified slightly from Robbins and Venables (1991).

Taxa	#1	2	3	4	5	6	7	8	9	10	11	12	13
<i>A. coelebs</i>	0	0	2	1	1	0	1	2	3	?	0	0	1
<i>L. barajo</i>	0	0	2	1	0	2	1	0	0	?	0	0	1
<i>J. rocena</i>	1	1	2	0	0	0	1	0	0	?	1	0	0
<i>J. adrienne</i>	0	0	2	1	0	0	1	0	0	?	1	1	0
<i>J. malvina</i>	0	0	2	1	1	1	1	1	1	?	1	1	0
<i>J. janthodina</i>	0	0	3	1	1	1	0	0	2	0	1	1	0
<i>J. cydonia</i>	0	0	3	1	1	1	0	0	2	1	1	1	0
<i>J. lea</i>	0	0	3	1	1	1	0	0	2	1	1	1	0
<i>J. armilla</i>	0	0	1	1	1	1	0	0	2	1	1	1	0
<i>J. janthina</i>	0	0	3	1	1	1	0	0	2	1	1	1	0
<i>J. sista</i>	0	0	2	1	1	1	0	0	2	1	1	1	0
<i>J. aurora</i>	0	0	1	1	1	1	0	0	2	2	?	?	0
<i>J. halli</i>	0	0	3	1	1	1	0	0	2	1	?	1	0
<i>J. flosculus</i>	0	0	0	1	1	1	0	0	2	2	1	1	0

CHARACTERS. 1. Length of male foreleg femur (0) shorter than length of tibia plus tarsus, (1) longer than length of tibia plus tarsus. 2. Male foreleg femur (0) without a scale brush, (1) with a scale brush. 3. Ratio of length of 2A divided by length from base of vein 2A to the forewing apex (0) >0.827, (1) >0.803 & <0.827, (2) >0.803 & <0.760, (3) <0.760. 4. Base of ventral hindwing (0) with a red spot, (1) with no red scales. 5. Ventral forewing (0) with androconial patch, (1) without androconial patch. 6. Ventro-lateral edge of tegumen (0) without processes, (1) with processes dorsal of valvae, (2) with process ventral of valvae. 7. Elbow of gnathos (0) with a keel-shaped ridge, (1) without a keel-shaped ridge. 8. Setae on valva (0) extend continuously to valva tip, (1) on valva tip & middle, but not in-between, (2) none at valva tip. 9. Ventral cornutus (0) absent, (1) arrowhead shaped, (2) "tongue-depressor" shaped, (3) slender. 10. Average width of the ventral "tongue depressor" shaped cornutus (0) <0.06 mm, (1) 0.06–0.16 mm, (2) >0.16 mm. 11. Ventral attachment of corpus bursae to ductus bursae (0) directly ventral of dorsal attachment, (1) > 0.25 mm more posterior than dorsal attachment. 12. Anterior lamella postvaginalis (0) without dorsal and ventral longitudinal striations, (1) with dorsal and ventral longitudinal striations. 13. Ventral hindwing anal angle (0) iridescent turquoise scales from vein Cu_1 to the inner margin, (1) without iridescent turquoise scales from Cu_1 to inner margin.

for types are given as they appear on data labels.

The character matrix with a list of the characters and their states are presented in Table 1. The ingroup species are *Janthecla rocena*, *J. adrienne* Robbins, *J. malvina* (Hewitson), *J. janthodina* (Dyar), *J. cydonia* (H. H. Druce), *J. lea* Venables & Robbins, *J. armilla* (H. H. Druce), *J. halli* Busby & Robbins, *J. janthina* (Hewitson), *J. sista* (Hewitson), *J. aurora* (H. H. Druce), and *J. flosculus* (H. H. Druce). The outgroup species are *Allosmaitia coelebs* (Herrich-Schäffer) and *Laothus barajo* (Reakirt), the type species of *Allosmaitia* and *Laothus* respectively (Table 1). The characters from the previous matrix (Robbins & Venables, 1991) were the basis of the current analysis. To accommodate character states occurring in the new species or in the outgroups, a few were modified slightly, and one new one was added (character 13). Quantitative multi-state characters 3 and 10 had been analyzed additively (ordered) (Robbins & Venables, 1991), but were analyzed both additively and non-additively

in this paper.

The implicit enumeration (ie*) option in Hennig86 software, which searches exhaustively for shortest trees, was used to analyze the character matrix, and a strict consensus tree of all most parsimonious trees was derived. To test the assumption of equally weighted characters, a successive weighting iteration was performed (Farris, 1969). Trees were imported into WinClada software (Nixon, 2002), where character state changes were mapped using the fast optimization option. Jackknife supports were determined in WinClada using Nona (100 replications with the mult*10 option, memory 100 trees). Distribution of *Janthecla* species (Table 2) is taken from Robbins and Venables (1991) and from the collections listed above.

RESULTS—NEW TAXA

The two species described below belong to the Eumaeini because they have 10 forewing veins,



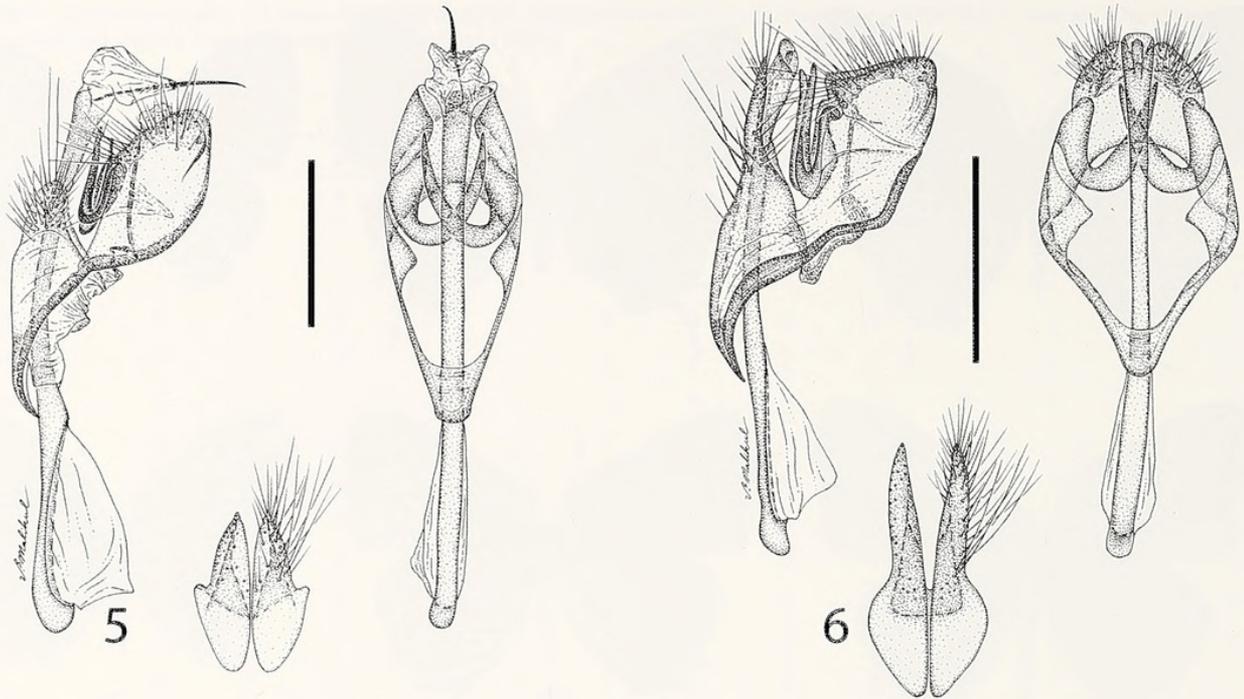
Figures 1-3. Adults of *Janthecla*, dorsal (top) and ventral wing surfaces. 1. ♂ *J. adrienne* (forewing length 16.4 mm). 2. ♀ *J. adrienne*. 3. ♂ *J. halli*.



Figure 4. Scales on frons, upturned in male *J. adrienne* (left) and downturned in male *J. halli*.

greyhound shaped male genitalia lacking a juxta, and a male foretarsus that is fused, stubby tipped, and used for walking (Eliot, 1973). *Janthecla adrienne* belongs to *Janthecla* because attachment of the female genitalia corpus bursae to the ductus bursae is more posterior ventrally than dorsally, a synapomorphy for

Janthecla that is unknown elsewhere in the Eumaeini (Robbins & Venables, 1991). *Janthecla halli* was placed in *Janthecla* (its female is unknown) because its ventral wing pattern and male genitalia are indistinguishable from some *Janthecla* species whose females possess the synapomorphy for *Janthecla*. It is distinguished



Figures 5-6. *Janthecla* male genitalia in lateral (left) and ventral aspects (with valvae illustrated separately for clarity). 7. *J. adrienne*. 8. *J. halli*. Scale 0.5 mm.

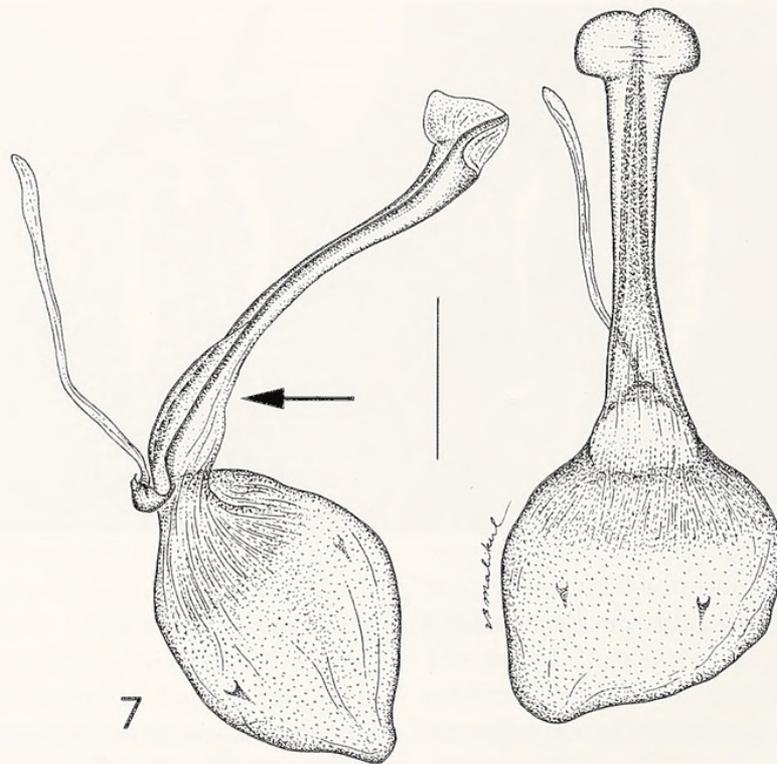


Figure 7. Female genitalia *J. adrienne* in lateral (left) and ventral aspects. Arrow points to ventral attachment of corpus bursae and ductus bursae. Scale 0.5 mm.

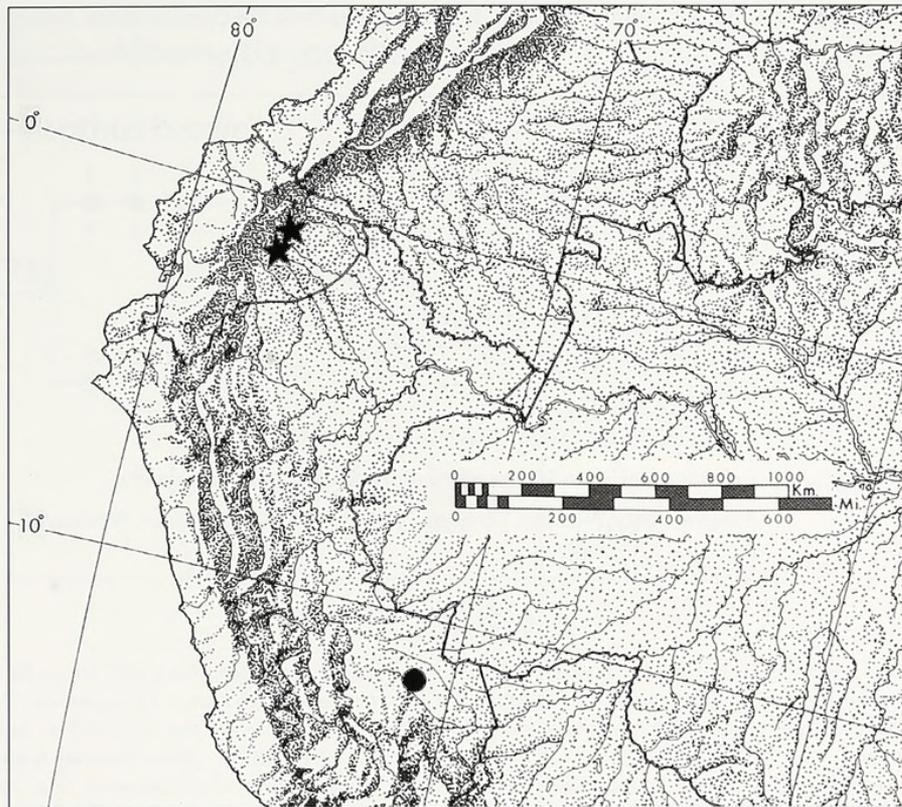


Figure 8. Distribution of *J. adrienne* (circle) and *J. halli* (star) in Peru and Ecuador.

from these species primarily by the pattern and scent patch on the dorsal forewing. Both new species share the extensive turquoise iridescent scaling at the anal angle of the ventral hindwing that is characteristic of *Janthecla*, but this scaling occurs in eumaeine genera not belonging to the *Allosmaitia* Section, most notably in *Oenomaus* Hübner and *Porthocla* Robbins.

Janthecla adrienne Robbins, n. sp.

Diagnosis. *Janthecla adrienne* is distinguished from all other *Janthecla* species by two characters. (1) The base of the ventral hindwing of *J. adrienne* has rust-brown scales bordered by a sinuate white line that is basally edged with black scales (Figs. 1-2). In *J. rocena*, the basal scales are red (illustrated in D'Abrera 1995: 1155). In the remaining *Janthecla* species (other than *J. adrienne* and *J. rocena*), the white line is straight and reduced in length (Fig. 3). This line is slightly curved in some individuals of *J. flosculus*, but it curves downwards towards the postmedian line, not towards the body, as in *J. adrienne* (Figs. 1-2). (2) *Janthecla adrienne* is the only *Janthecla* species with scales on the frons directed upwards, not downwards (Fig. 4).

Identification. In addition to the two diagnostic characters, males of *J. adrienne* are distinguished by their androconia and foreleg. *Janthecla rocena* and *J. adrienne* are the only *Janthecla* with black androconia on the ventral forewing (Fig. 1), but *J. adrienne* lacks the modification of the male foreleg of *J. rocena*, which was detailed in Robbins and Venables (1991).

Description of Male. *Frons* (Fig. 4). Slender brown scales

oriented upwards with a few broad white scales intermixed. Lateral edges of frons with white scales. *Antennae.* Stalk with about 18 white ringed segments. Club incrassate with about 17 segments. Yellow or orange nudum continuous on the club and as isolated patches on some segments of the stalk, as is often the case in eumaeines (Eliot 1973). *Mean forewing length* 14.4 mm, SD=0.56, N=3. *Wing Pattern.* As illustrated (Fig. 1). *Androconia* (Fig. 1). Like *J. rocena*, this species has black androconia on the ventral forewing where the hindwing overlaps it, but lacks dorsal forewing androconia. *Legs.* The foreleg is similar in morphology to that of *J. janthina*, not to that of *J. rocena*. Both foreleg structures were illustrated in Robbins and Venables (1991). *Genitalia.* As illustrated (Fig. 5).

Description of Female. *Frons.* Slender yellowish, light brown scales oriented upwards. Lateral edges of frons with white scales. *Antennae.* Same as male. *Mean forewing length* 14.5 mm, SD=0.45, N=2. *Wing Pattern.* As illustrated (Fig. 2). *Genitalia.* As illustrated (Fig. 7).

Types. *Holotype* (Fig. 1). ♂ Peru, M. de Dios, Parque Manu, Pakitza, 11°55'48"S, 71°15'18"W, 340 m, 4 Oct 1991, Leg. R. Robbins. Deposited MUSM. *Paratypes.* 1♂ same locality and collector as holotype, 11 Oct 1991 (DZUP). 1♂ Perú, M. de Dios, Parque Manu, Pakitza, 11°53'S, 70°58'W, 400 m, 12 Oct 1990 (USNM). 1♀ same locality as holotype, 14 Oct 1991, Leg. O. Mielke (USNM). 1♀ (Fig. 2) same locality and collector as holotype, 12 Oct 1991 (MUSM).

Other Specimen. About 13 years ago, Christian Brévignon sent Robbins a photograph of a specimen from French Guiana labeled "Saül, November 1975" from the collection of R. P. Barbotin (Cayenne). The wing pattern and androconia are nearly identical to those of *J. adrienne*. We have not been able to examine this specimen to be certain that it is the same species.

Etymology. This beautiful species is named for Adrienne

Table 2. Distribution of *Janthecla* species. "Amazon Basin" refers to areas from the Orinoco to the Amazon drainages.

<i>J. rocena</i>	Mexico to Southern Brazil
<i>J. adrienne</i>	Amazon Basin
<i>J. malvina</i>	Amazon Basin, Coastal Brazil
<i>J. sista</i>	Amazon Basin
<i>J. armilla</i>	Coastal Brazil
<i>J. aurora</i>	Coastal Brazil, Northeast Argentina
<i>J. flosculus</i>	Southern Brazil
<i>J. janthodonia</i>	Northern Central America
<i>J. cydonia</i>	Southern Central America to Western Ecuador
<i>J. janthina</i>	Central America to Western Ecuador and Northern Venezuela
<i>J. leea</i>	Amazon Basin, Western Ecuador (JHKW & RCB), Northern Venezuela
<i>J. halli</i>	Upper Amazon Basin

Venables, the co-describer of *Janthecla*. Her untimely death in 1994 was a tremendous loss for entomology. The name of this species is a noun in apposition, as Adrienne would have wanted it. It is indeclinable and non-latinized.

Type locality. Pakitza is a field station in Peru's Manu Biosphere Reserve that was run by the Smithsonian Institution's Biodiversity of Latin America Program in conjunction with various Peruvian academic institutions. Although the types from 1990 and 1991 have slightly different coordinates and elevations, they were collected in the same area. The data labels from 1991 are more accurate (Wilson & Sandoval, 1996).

Habitat and Seasonality. Pakitza is lowland primary forest. Aspects of its flora, fauna, and anthropology were detailed in Wilson and Sandoval (1996). The types were collected in October during the transition from the dry to wet seasons (when the most light reaches the forest floor) in the understory along trails through the forest. Most field work at Pakitza was done in October.

Distribution (Fig. 8). If the photographed specimen mentioned above is *J. adrienne*, as appears to be the case, then this species occurs over most of the vast expanse of lowland rainforest from Peru to French Guiana.

Janthecla halli Busby & Robbins, n. sp.

Diagnosis. *Janthecla halli* is distinguished by the dorsal forewing wing pattern and by the color, placement, and size of the dorsal forewing androconial patch (Fig. 3). A broad black border covers the outer half of the forewing and the anterior wing from the costal margin to vein M_2 . The triangular inner portion of the forewing is covered with brilliant blue scales and an iridescent dark green androconial patch located between the basal blue and the black border. Although the androconial patches of other *Janthecla* may reflect a greenish hue when viewed at different angles, such as the outer edge of the patch in *J. sista*, none have the androconial patch entirely iridescent dark green. The androconial patch of *J. halli* extends from vein M_2 to Cu_2 with at least some androconia in wing cell Cu_2-2A . The only other *Janthecla* with androconia in wing cell Cu_2-2A is *J. sista*. In worn specimens (including two of the paratypes of *J. halli*) the androconial patches have lost most of the green iridescence, but the position of the patch is essentially the same in all of the types and differs from that of all other *Janthecla*.

Description of Male. **Frons** (Fig. 4). A mixture of slender and broad brown scales oriented downwards. Lateral edges of frons with

white scales. **Antennae.** Stalk with about 16 white ringed segments. Club incrassate with about 14 segments. Yellow and dark orange nudum continuous on the club and as isolated patches on some segments of the stalk. **Mean forewing length.** 14.4 mm, SD=0.56, N=4. **Wing Pattern.** As illustrated (Fig. 3). **Androconia** (Fig. 3). As noted in the diagnosis. **Legs.** The foreleg femur and tibia are similar in morphology to those of *J. janthina* (illustrated in Robbins & Venables, 1991). **Genitalia.** As illustrated (Fig. 6).

Female. Associating males and females of many *Janthecla* species is difficult (Robbins & Venables, 1991). Recognition of female of *J. halli* will probably require finding an adult pair *in copula*, rearing male and female siblings, or comparing DNA sequences of both sexes.

Types. **Holotype** (Fig. 3). 1♂ Ecuador, Napo Prov, 4 km Tena-Pano Rd., 1°02'S, 77°50'W, 600 m, 28 Sept 1990, S. S. Nicolay leg (USNM). **Paratypes.** 1♂ Ecuador, Pastaza, 10 km SW Puyo, 1°34'S, 78°02'W, 1000 m, 18 September 1990, S. S. Nicolay leg (MECN). 1♂ E. Ecuador, Napo Province, km 20 Tena-Puyo, Apuya, 600 m, 19/10/96, collected by: J. P. W. Hall & K. R. Willmott (JHKW). [Note: the Apuya locality is now at km 14, not km 20]. 1♂ Ecuador, Napo Province, 4 km W of Misahuallí, 450 m, 19-20.x.1995, leg. R. Busby (RCB). 1♂ Ecuador, Napo Province, 4 km W of Misahuallí, 450 m, 16-18.x.1991, leg. R. Busby (RCB). 1♂ Ecuador, Napo Province, Misahuallí, X-24-98, Ann Albright (OSU).

Etymology. This species is named for Jason P. W. Hall, who independently recognized it as a distinct species. Jason has made prodigious contributions to our knowledge of South American butterflies, especially Riodinidae.

Type locality. David Ahrenholz accompanied S. S. Nicolay on the trip during which the holotype was collected. He kindly provided the following description of the type locality as it was in 1990: "4 km after leaving Tena on the right side of the road was a path leading towards the Río Pano. From the road, the path cut between two fincas before dropping steeply (15 m) to a stream. The path continued beyond the stream past a school (about 600 m from the road) to the river. The area was very disturbed. A narrow band of secondary trees bordered the main road, followed by a large coffee finca, then more secondary forest down to the stream and beyond."

Paratype localities. The two paratypes collected by Busby were found along a shady hedgerow during the early afternoon. The hedgerow, which contained a few remnant large trees, separated an overgrown cow pasture from a finca planted with citrus trees and a few coffee plants. The hedgerow was located at least 500-1000 m

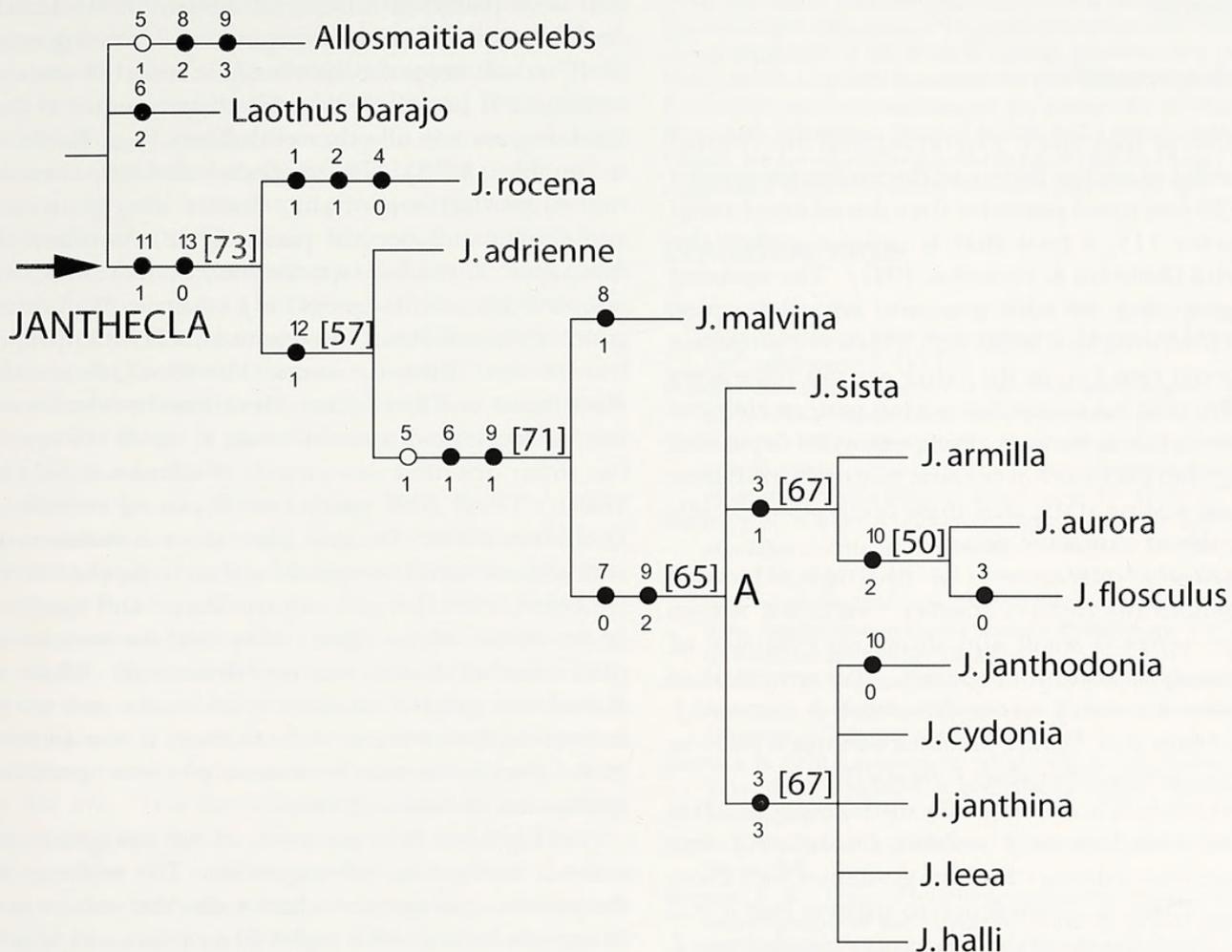


Figure 9. Cladogram for *Janthecla*. Characters 3 and 10 were analyzed additively. *Allosmaitia coelebs* and *Laothus barajo* are outgroups. Character numbers are placed above nodes and character state numbers below nodes. Open circles represent reversal or convergence of the character state at that node. Jackknife support is noted in brackets. When characters 3 and 10 were analyzed non-additively, this tree was one of the four shortest. Topology of a strict consensus of the four trees differs only in the collapse of the node noted by A.

from the nearest tract of "secondary" forest.

Jason Hall kindly provided the following description of the locality where the paratype from Apuya was found. "It was collected atop a broad ridge cloaked with disturbed wet rainforest. It was flying about 1 m above the ground just inside the forest edge in the early afternoon."

Distribution (Fig. 8) and **Seasonality.** *Janthecla halli* is known from 450-1,000 m elevation at the eastern base of the Ecuadorian Andes during the months of September and October.

RESULTS—PHYLOGENETIC ANALYSIS

Addition of the new taxa and outgroups did not change the cladogram topology from the previous analysis (Robbins & Venables, 1991) except for the additional taxa. Parsimony analysis with characters 3 and 10 additive (ordered) resulted in one cladogram

with 21 steps, a consistency index of 95, and a retention index of 95 (Fig. 9). Character 5 (presence or absence of a ventral forewing androconial patch) was homoplastic, but successive weighting did not change the cladogram topology. The species from *J. janthodonia* to *J. halli* in the cladogram (Fig. 9) differ in the pattern of the dorsal forewing, including the androconia, but we were unable to code this pattern variation in a phylogenetically informative fashion. When the phylogenetic analysis was repeated with characters 3 and 10 non-additive (unordered), there were four equally parsimonious cladograms of length 21 steps, one of which was the same as the illustrated cladogram (Fig. 9). The strict consensus of these four collapses the trichotomy at node A (Fig. 9) into a nine-species bush.

DISCUSSION

Janthecla systematics

Janthecla had been characterized by ventral attachment of corpus bursae to ductus bursae greater than 0.25 mm more posterior than dorsal attachment (character 11), a trait that is unique within the Eumaeini (Robbins & Venables, 1991). The updated phylogeny (Fig. 9) adds a second synapomorphy; ventral hindwing anal angle with iridescent turquoise scales from vein Cu_1 to the inner margin (character 13). This trait is a conspicuous wing pattern element of *Janthecla*, but its status as a synapomorphy depended on outgroup information because extensive iridescent turquoise scaling at the anal angle occurs sporadically in a variety of eumaeine genera.

Janthecla adrienne is a biologically and phylogenetically distinct species. Variation within the type series is small and shows no evidence of intergradation with other species. It is sympatric at its type locality with *J. rocena*, *J. malvina*, *J. sista*, and *J. lea* (Robbins *et al.* 1996). *Janthecla adrienne* is sister to the entire genus other than *J. rocena* (Fig. 9).

Janthecla halli is a biologically distinct species. It is sympatric with *J. rocena*, *J. malvina*, *J. sista*, and *J. lea*, but there is no evidence for intergradation with these species. There is no evidence to suggest that it is a geographical variant of the allopatric *J. janthodonia*, *J. cydonia*, or *J. janthina* (Fig. 9). For these reasons, we recognize *J. halli* as a distinct biological species even though its phylogenetic position within the genus is not fully resolved (Fig. 9).

Allosmaitia section, upright frons scales, and the placement of *Evenus*.

Janthecla was placed in the *Allosmaitia* Section of Eumaeini with *Laothus* and *Allosmaitia* (Robbins, 2004b). Although no synapomorphy for this group has been proposed, this placement was based on similar structure of the male genitalia (*cf.* illustrations in Clench, 1964; Salazar & López, 1996) and androconia on the posterior ventral forewing in some species of each genus. With the discovery of upright frons scales in *J. adrienne* (Fig. 4), a third character common to *Janthecla* and *Laothus* has been found.

Scales on the frons are oriented downwards in the Eumaeini except for three genera in which upright frons scales occur in some species and not others. (1) *Laothus oceia* (Godman & Salvin), *L. laothoe* (Godman & Salvin), and *L. erybathis* (Hewitson) have upright oriented frons scales while *L. barajo* (Reakirt) does not (Godman & Salvin, 1887). Despite this variation, all

four were placed in *Laothus* (Robbins, 2004b) based on the proposed synapomorphy that hindwing vein $Sc+R_1$ terminates at the middle of the costa (illustrated in Salazar & López, 1996) while it terminates at the hindwing apex in all other eumaeines (e.g., Robbins & Venables, 1991). These species also share nearly indistinguishable genitalia, similar wing patterns, and similar androconial patches. (2) As noted in this paper, all *Janthecla* species have their frons scales oriented downwards except for *J. adrienne*. (3) A third genus, *Evenus* Hübner, also has members with upright frons scales. *Evenus coronata* (Hewitson), *E. teresina* (Hewitson), and *E. temathea* (Hewitson) have scales on the frons oriented upwards while *E. regalis* (Cramer) has them oriented downwards (Godman & Salvin, 1887). These four species were placed in *Evenus* (Robbins, 2004b) because they share a number of androconial, larval foodplant, and genitalic characters (Robbins, 2004a), especially the shape and number of the spines of the signa. However, the systematic placement of *Evenus* was problematical. While it shared the upward oriented frons scales and some androconial structures with *Laothus*, it was placed in the *Brangas* Section because of phenetic genitalic similarities (Robbins, 2004b).

Phylogenetic interpretation of the upright frons scales is ambiguous, but suggestive. The evidence in the previous paragraph indicates that the occurrence of upright frons scales is highly homoplastic, for which reason this character provides little phylogenetic information (e.g., Farris, 1969). Accordingly, *Evenus* was not placed in the *Allosmaitia* section of the Eumaeini (Robbins, 2004b). Alternately, the "tendency" for frons scales to be upright is consistent with the placement of *Laothus* and *Janthecla* in the same section and suggests that *Evenus* may also belong to the *Allosmaitia* Section. The hypothesis that this "tendency" evidence is informative will depend upon support from independent character evidence, such as DNA sequences.

Diversification

During the time that the ancestor of the *J. sista* clade (node A on Fig. 9) diversified into nine extant species, ancestors of *J. malvina*, *J. adrienne*, and *J. rocena* did not speciate, at least as represented by known extant species. However, poor phylogenetic resolution within the *J. sista* group and unrecorded larval food plants allow only a few comments about the relatively rapid diversification within this clade. The ventral wing pattern and genitalia of all nine species of the *J. sista* group are nearly indistinguishable. Up to three species of this group may be sympatric (Table 2). Adults of these sympatric species occur in the same

habitats, oftentimes are found flying within a few meters of each other, and cannot be distinguished by their behavior. These results suggest that a “lock-and-key” mechanism (Shapiro & Porter, 1989), mate recognition of small differences in the ventral wing patterns (Fordyce *et al.*, 2002), and habitat partitioning are unlikely to have been pertinent factors in the diversification of this clade. Indeed, the only evident differences among members of the *J. sista* clade (and basically the only way to distinguish the species) are aspects of the dorsal wing pattern and dorsal forewing androconia. These dorsal wing differences are presumably related to courtship, and if so, might well be a prime factor in the relatively rapid diversification of *J. sista* and relatives.

Postscript. On 21 September 2006, RCB recorded more information about *J. halli*. The site was a hilltop (950 m) approximately 3 km west of Mendez, Morona Santiago Province, Ecuador. The hill was mainly cow pasture (waist-high grass) with a small remnant of secondary forest on the summit and one hillside. Late in the day, several hairstreaks were flying about each other above a small bush (2 meters high) between the forest and cow pasture on the east (shady) side of the hill. This behavior is typical of males setting up mating territories. Between 1600 and 1615 hours, three males of *J. halli* were collected, each on the top leaf of the bush they had been circling. A second visit to this site on 1 October 2006 yielded one more male on the same bush at 1615 hours. At 1625 hours, another *Janthecla* flew to the bush. It landed for two seconds, flew about seven meters, landed momentarily, returned to the original bush for a couple of seconds, landed on a smaller bush about three meters distant at the edge of the cow pasture, and was collected. It was a female. Yet another individual circled the original bush at 1655 hours, but then flew away.

The discovery of *J. halli* in Mendez represents a 135 km range extension southward but is otherwise not surprising. As with previous specimens from localities near Misahualli, Tena and Apuya, this site was disturbed and shady. While the flight time in Mendez is later in the day than the time when other individuals were collected, it is the first record of presumed territorial behavior in this species. The association of the female with the males depends upon the behavioral observations noted above. We do not yet know if this female can be distinguished morphologically from females of sympatric *J. leea* and *J. sista*.

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